A COMPARATIVE STUDY OF THE PRODUCTION OF EGGS IN EIGHT PARDOSA SPECIES IN THE FIELD (ARANEAE, LYCOSIDAE)

by

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ABSTRACT

The egg production of eight common *Pardosa* species in the Netherlands, estimated from field samples, is described. Samples were taken on the same spot during five years for six species (1966—1970). In 1968 some species were sampled extensively in several parts of the Netherlands. Intra- and interspecific differences in egg production were found to be related to the size of the mother spiders. Factors influencing intraspecific differences in size of the spiders are discussed.

INTRODUCTION

The relation between food consumption and egg production in spiders has been dealt with by Turnbull (1962) in *Linyphia triangularis*. Data on Lycosid spiders in general are scarcely known (cf. Edgar, 1968, 1971). Kessler (1971) studied this relationship in four species of *Pardosa* under experimental conditions. These results, however, should be compared with data on natural populations. This paper deals with data on egg production of eight species of *Pardosa* in the field, estimated from samples taken in natural populations. The results are discussed in relation to data from the literature as well as in relation to experimental data (Kessler, 1971; Turnbull, 1962, 1965).

MATERIAL AND METHODS

All samples were made by hand-collecting female spiders carrying egg sacs. Care was taken to collect specimens in the period when all females were carrying egg sacs, viz., in the middle of the reproductive period, so that a sample is representative for all females in the population.

Eight species were sampled in 1968 in different localities throughout the country, six species were sampled from 1966 to 1970 yearly in the same locality.

A description of the habitat of the species concerned in the Netherlands is given by Richter (1970).

It is only possible to collect spiders in sufficient quantities when the weather is bright. This seriously narrows down the time available for sampling. Moreover, the period in which the females are carrying the egg sacs is about the same for all species (the middle of May until the end of June). For these reasons some samples in the series are missing or incomplete.

In each sample a number of spiders were collected which were missing one or more legs. The egg sacs of these specimens are not considered in this paper. The same holds

for egg sacs containing egg sac parasites (Hymenoptera). The latter are dealt with elsewhere (Kessler & Fokkinga, 1973).

Every specimen collected was kept separately, so that relations between mother spider and offspring could be studied.

A positive correlation between size of the mother spider and number of offspring has been demonstrated in the genus *Pardosa* by Petersen (1950). In order to investigate this phenomenon interspecifically one should either calculate regression lines for each species or express the number of eggs as a ratio of spider size. The latter method is used in this paper because the calculations are simple and the method gives a more direct insight, when comparisons are made interspecifically. The dryweight of carapaces, including the legs, is used as an estimate for spider size. Carapaces were dried in an oven at 60° C.

For statistical method Duncan's new multiple range test with Kramers modification for inequal sample size was used ($\alpha = 0.05$).

RESULTS

I. Comparison of the species

In 1968, the eight common species of *Pardosa,* viz., *Pardosa amentata* (Clerck), *P. lugubris* (Walck.), *P. pullata* (Clerck), *P. prativaga* (L. Koch), *P. nigriceps* (Thorell), *P. purbeckensis* F.O.P.-Cambridge, *P. monticola* (Clerck) and *P. palustris* (L.), were sampled in order to compare the species as to the amount of egg production.

The data on numbers of eggs per egg sac (1), the dryweight of the carapaces (2) and the numbers of eggs per mg carapace dryweight (3) are shown together in table 1 and are discussed separately in the following chapters.

a. Number of eggs

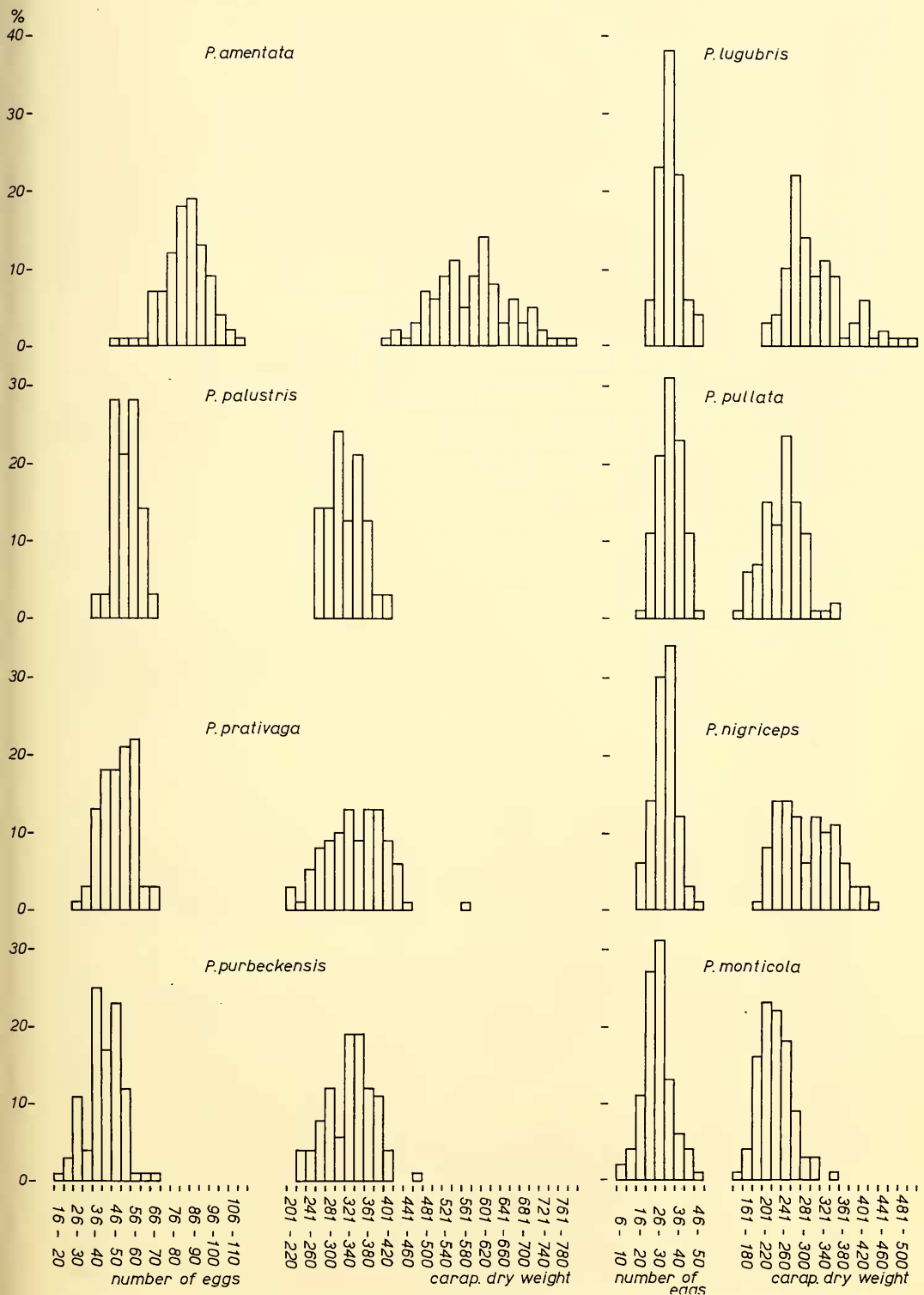
The mean numbers of eggs in the egg sacs range from 86.2 in *P. amentata* to 26.6 in *P. monticola.* In Graph 1 the frequencies are shown; Graph 2 gives the range of the values and the means for all species together. Three separate groups can be distinguished (though sometimes a considerable overlap has been found).

P. amentata	± 85 eggs
P. palustris, P. prativaga and *P. purbeckensis*	± 50 eggs
P. lugubris, P. pullata, P. nigriceps and *P. monticola*	± 30 eggs

In some egg sacs undeveloped eggs were found. They are easily recognized, even at very early stages in the development of the egg batch, by a brownish colour (normal eggs are white). Table 1 illustrates that the number of undeveloped eggs is never high. The great varibility is due to the fact, that in most egg sacs only 1 or 2 undeveloped eggs are found, whereas in a few others more than half of the eggs are undeveloped.

b. Size of spiders (carapace dryweight)

The differences in carapace dryweight between the species are rather small, with the exception of *P. amentata* (Table 1). None of the species does show any overlap in values with *P. amentata* (Graph 1). In this group of species *P. monticola* and *P. pullata* can



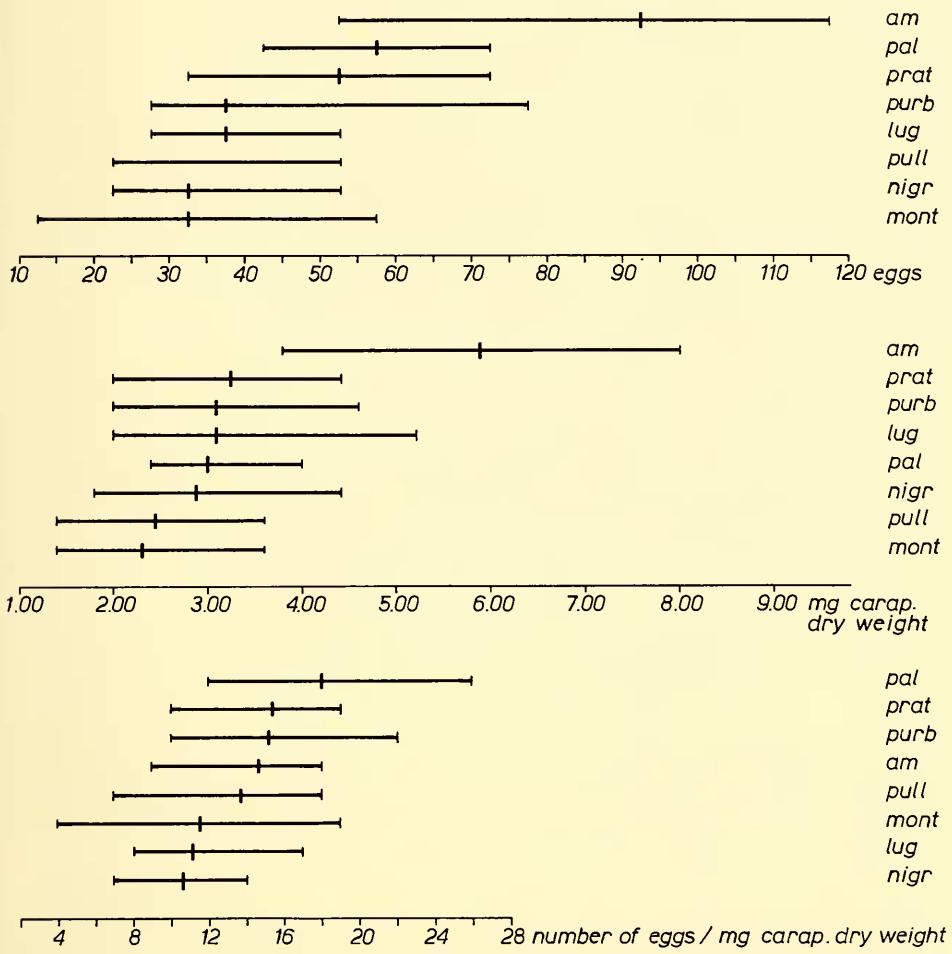
Graph 1. Frequency diagrams of the number of eggs and the dryweight of the carapaces (in 0.01 mg) of eight *Pardosa* species

Table 1. Comparison of the egg production and size of eight species of *Pardosa* in 1968. Means and standard deviations are given. In table 1a the statistical significance of the differences in mean values are given. The names of the spiders represent the values. Any two values not flanked by the same line are significantly different. (am = *P. amentata*, pal = *P. palustris*, prat = *P. prativaga*, purb = *P. purbeckensis*, lug = *P. lugubris*, pull = *P pullata*, nigr = *P. nigriceps*, mont = *P. monticola*)

Spider species	Number of specimens	Number of eggs	Dryweight of carapace in mg	Number of eggs per mg carapace dryweight	Number of egg sacs containing undeveloped eggs	Mean number of undeveloped eggs in these egg sacs
P. amentata	91	86.2 ± 12.9	5.90 ± 0.81	14.7 ± 1.6	19	3.1 ± 3.3
P. palustris	29	54.2 ± 6.9	3.03 ± 0.36	18.0 ± 2.4	6	2.3 ± 2.8
P. prativaga	78	49.3 ± 8.3	3.25 ± 0.63	15.4 ± 2.2	20	2.2 ± 1.2
P. purbeckensis	75	47.1 ± 8.9	3.12 ± 0.49	15.2 ± 2.5	46	3.6 ± 2.6
P. lugubris	90	33.9 ± 6.1	3.11 ± 0.63	11.1 ± 1.8	7	2.9 ± 3.7
P. pullata	81	33.1 ± 6.1	2.44 ± 0.43	13.7 ± 2.1	8	1.4 ± 1.1
P. nigriceps	73	30.4 ± 5.6	2.92 ± 0.58	10.6 ± 1.6	7	2.1 ± 1.9
P. monticola	97	26.6 ± 7.7	2.29 ± 0.36	11.6 ± 2.9	8	1.3 ± 0.5

Table 1a. For legends see table 1

Number of eggs	Dryweight of carapace	Number of eggs per mg carapace dryweight
am	am	pal
pal	prat	prat
prat	purb	purb
purb	lug	am
lug	pal	pull
pull	nigr	mont
nigr	pull	lug
mont	mont	nigr



Graph. 2. Range of values and means of number of eggs per egg sac, carapace dryweight and number of eggs per mg carapace dryweight of eight *Pardosa* species. (For further explanation see table 1.)

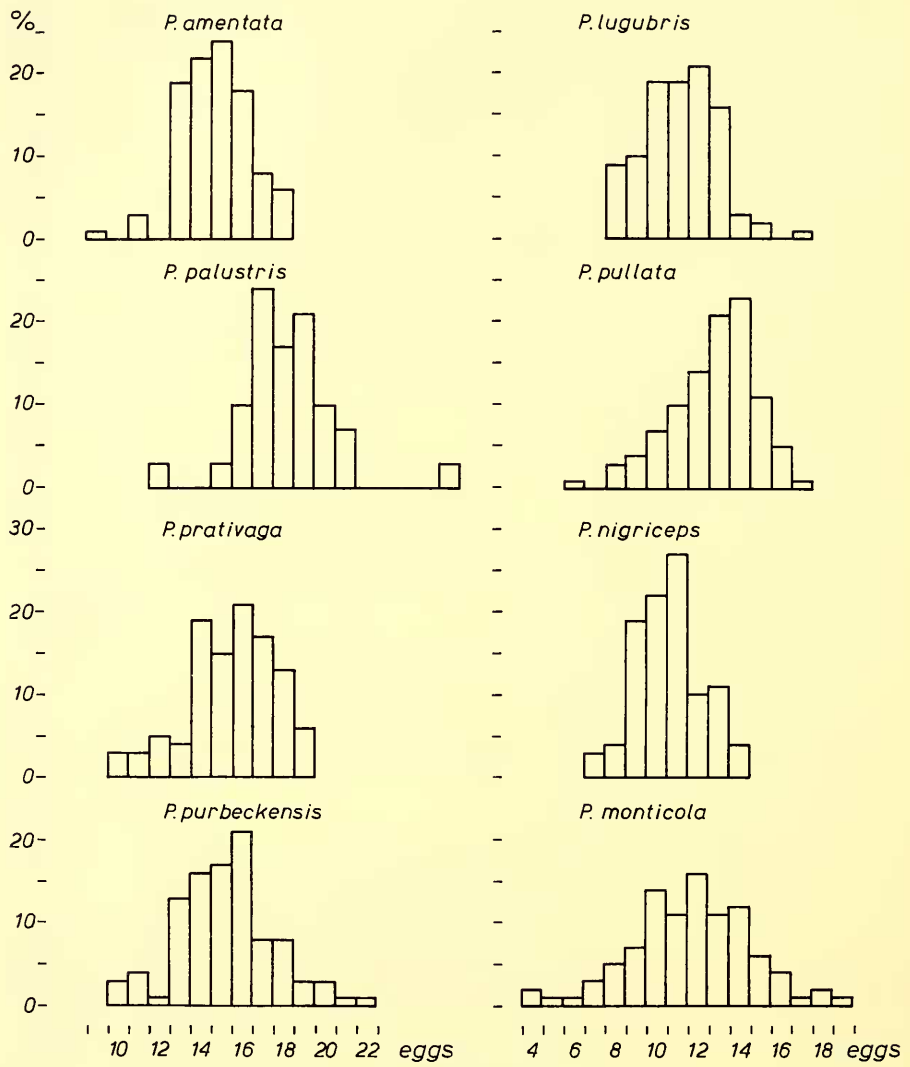
be distinguished by their carapace weight (2.3 and 2.4 versus ± 3 mg). Furthermore it should be noted that in most species different size groups are found (Graph 1).

Probably these differences are caused by the presence of spiders born from the first egg sacs as well as from the second egg sacs of last year.

c. Number of eggs per mg carapace dryweight

The data in table 1, Graph 2, and Graph 3, show that any differences in the values of number of eggs per mg carapace dryweight are not conspicuous. This leads to the conclusion that in general the size of the spider species determines the number of offspring.

An exception is found in *P. palustris*. In this species, under field conditions, considerably more eggs are produced per unit of size than in the other species. This is in



Graph 3. Frequency diagrams of the number of eggs per milligram carapace dryweight of eight *Pardosa* species

agreement with the data of Kessler (1971), which showed that under experimental conditions *P. palustris* produces more eggs per unit of size than the other investigated species, because the eggs are lighter.

II. Comparison of samples from different localities in the same year

Samples from different localities in 1968 (Fig. 1) were avaiable from *P. amentata, P. pullata, P. purbeckensis, P. nigriceps, P. monticola* and *P. prativaga.* The results are shown in table 2.

Fig. 1. The geographic position of the different sampling localities in the Netherlands in 1968 (1 = Schiermonnikoog, 2 = Weerribben (*P. prativaga*), 3 = IJsselmeerpolder, 4 = Surroundings of Amsterdam (*P. amentata*), 5 = *Hollandsche Rading*, 6 = Oostvoorne)

a. Number of eggs.

In *P. amentata* the mean number of egg in locality 4 is relatively low (62.9). The difference between the other three localities (72.9—86.2) are not conspicuous. The localities 1, 2 and 3 are situated in the normal habitat of *P. amentata* in the Netherlands, viz. along ditches in meadows. Locality 4 is a piece of wasteland with heaps of black earth along a ditch. The density of *P. amentata* is relatively high there. In this locality the same number of specimens as at the other localities was collected in a much shorter period.

In *P. pullata* only locality 5 shows a very low number of eggs per egg sac (24.5). These specimens were collected on small, newly formed dunes, near the beach of the Frisian island Schiermonnikoog. The other localities (1 to 4) are situated on Schiermonnikoog and in Hollandsche Rading.

In *P. purbeckensis* two groups can be distinguished, on account of the number of eggs: spiders from localities 1 and 2 (65.0 and 58.1 eggs) and from 3 and 4 (47.1 and 42.8 eggs). Localities 3 and 4 are situated in the normal habitat of the species, viz., salt marshes between tidal creeks on Schiermonnikoog. Locality 1 is situated in a recently made polder in the IJsselmeer; locality 2 on the island Oostvoorne, where a tidal salt marsh is enclosed by a dike.

In *P. nigriceps* the only difference between the localities is their geographical position:

Table 2. Data on egg sac samples from different localities in 1968. Any two values not flanked by the same line are significantly different

Spider species	Locality	Number of eggs	Dryweight of carapace	Number of eggs per mg carapace (dryweight)	Number of specimens
P. amentata	1	86.2 ± 12.9	5.90 ± 0.81	14.7 ± 1.6	91
	2	78.0 ± 10.8	5.80 ± 0.97	13.5 ± 1.0	18
	3	72.9 ± 14.8	5.87 ± 1.08	12.5 ± 2.2	44
	4	62.9 ± 9.2	5.33 ± 0.67	11.9 ± 1.5	146
P. pullata	1	33.1 ± 6.1	2.44 ± 0.43	13.7 ± 2.1	81
	2	30.0 ± 5.8	2.26 ± 0.44	13.3 ± 1.6	21
	3	28.3 ± 6.1	2.03 ± 0.37	13.9 ± 2.0	86
	4	26.6 ± 3.9	2.04 ± 0.30	13.0 ± 1.7	23
	5	24.5 ± 6.7	1.93 ± 0.15	12.8 ± 3.5	8
P. purbeckensis	1	65.0 ± 10.2	4.00 ± 0.82	16.3 ± 2.5	13
	2	58.1 ± 13.6	3.71 ± 0.38	15.7 ± 2.6	14
	3	47.1 ± 8.9	3.12 ± 0.49	15.2 ± 2.5	75
	4	42.8 ± 9.4	3.00 ± 0.46	14.3 ± 2.4	72
P. nigriceps	1	35.5 ± 4.7	2.96 ± 0.41	13.0 ± 1.1	94
	2	30.4 ± 5.6	2.92 ± 0.58	10.6 ± 1.6	73
P. monticola	1	30.8 ± 7.7	2.38 ± 0.46	12.9 ± 2.8	39
	2	26.6 ± 7.7	2.29 ± 0.36	11.6 ± 2.9	97
P. prativaga	1	59.3 ± 9.7	3.54 ± 0.54	16.8 ± 2.0	28
	2	49.3 ± 8.3	3.25 ± 0.63	15.4 ± 2.2	78

Oostvoorne (1) versus Schiermonnikoog (2). The same holds for *P. monticola:* Hollandsche Rading (1) versus Schiermonnikoog (2).

In *P. prativaga* locality 1 is the normal habitat of the species in the eastern part of the Netherlands, while locality 2 is the same as locality 2 of *P. purbeckensis* (Oostvoorne).

b. Size of spiders (carapace dryweight).

As the localities in table 2 are arranged according to decreasing mean number of eggs, it is easy to see in column 2 of table 2 that the dryweight of the carapace decreases in relation to the number of eggs. The same applies here as to the mean number of eggs in the different species (c.f. paragraph a).

c. Number of eggs per mg carapace dryweight.

In general the number of eggs per mg carapace dryweight shows the same trend as the dryweight of the carapace and the number of eggs, except in *P. pullata,* where there are no significant differences in the values (table 2).

A decreasing number of eggs corresponds with a decrease in size and a decrease in number of eggs per mg carapace dryweight. It seems that there is a correlation between size and number of eggs per unit of size. This correlation, however, could not be demonstrated in separate samples. This implicates that the values for carapace dryweight and number of eggs per mg carapace dryweight vary independently of each other. This does not mean that the reason why spiders in some localities stay smaller and produce less eggs per unit of size cannot be found in the correlation between size and number of eggs per unit of size.

III. Comparison of samples from the same localities in subsequent years

From some localities — the specific habitats of the species concerned — each year, from 1966 to 1970, a sample of females with egg sacs was taken. This was done for *P. amentata, P. pullata, P. nigriceps, P. purbeckensis, P. monticola, P. lugubris* and *P. palustris* (the last species only in 1966 and 1968). The results are shown in table 3.

a. Number of eggs.

It is clear from table 3, that in general the mean number of eggs in a population is kept at a fairly constant level. In each species there are no significant differences in numbers of eggs in different years. Most striking is the situation in *P. pullata* and *P. lugubris* where in 4 out of 5 and 3 out of 4 years, respectively, almost the same mean numbers of eggs were found. *P. amentata* is more or less an exception since the numbers of eggs agree for two years at the most. In the case of *P. palustris* no conclusions can be drawn because of lack of data.

However, it is clear that in some years either comparatively high or low values occur. From column 6 in table 3, it is concluded that there are no specific "good" or "bad" years for the whole group of species.

b. Carapace dryweight.

A constancy in carapace dryweight during the years has been found. This seems to agree with the data on the mean number of eggs, although they are not directly

Table 3. Data on egg production during subsequent years (in the last three columns the statistical significance of the difference in mean values is given). Two values not flanked by the same line are significantly different

Spider species		Number of eggs	Dryweight of carapace mg	Number of eggs per mg carapace (dryweight)	Number of specimens	Number of eggs	Carapace dryweight	Number of eggs per mg carapace dryweight
P. amentata	1966	74.4 ± 14.0	5.00 ± 0.98	15.0 ± 1.9	72	1968 86.2	1968 5.90	1966 15.0
	1967	81.5 ± 12.4	5.78 ± 0.65	14.2 ± 1.8	77	1970 84.3	1967 5.78	1970 14.9
	1968	86.2 ± 12.9	5.90 ± 0.81	14.7 ± 1.6	91	1967 81.5	1969 5.69	1968 14.7
	1969	73.7 ± 13.1	5.69 ± 0.80		12	1966 74.4	1970 5.69	1967 14.2
	1970	84.3 ± 14.5	5.69 ± 0.81	14.9 ± 1.9	56	1969 73.7	1966 5.00	
P. pullata	1966	33.9 ± 7.6	2.25 ± 0.33	15.3 ± 2.6	59	1966 33.9	1968 2.44	1966 15.3
	1967	33.8 ± 7.0	2.36 ± 0.46	14.2 ± 2.5	102	1967 33.8	1970 2.43	1967 14.2
	1968	33.1 ± 6.1	2.44 ± 0.43	13.7 ± 2.1	81	1970 33.4	1967 2.36	1968 13.7
	1969	28.9 ± 5.6	2.29 ± 0.27	12.8 ± 1.8	45	1968 33.1	1969 2.29	1970 13.6
	1970	33.4 ± 6.6	2.43 ± 0.43	13.6 ± 1.8	46	1969 28.9	1966 2.25	1969 12.8
P. nigriceps	1966	34.9 ± 5.6	3.30 ± 0.54	10.8 ± 2.0	99	1967 37.8	1966 3.30	1967 11.9
	1967	37.8 ± 5.8	3.20 ± 0.60	11.9 ± 1.7	113	1966 34.9	1967 3.20	1970 11.3
	1968	30.4 ± 5.6	2.92 ± 0.58	10.6 ± 1.6	73	1970 31.9	1968 2.92	1969 11.2
	1969	31.5 ± 5.5	2.88 ± 0.50	11.2 ± 2.0	48	1969 31.5	1969 2.88	1966 10.8
	1970	31.9 ± 5.2	2.88 ± 0.43	11.3 ± 1.6	40	1968 30.4	1970 2.88	1968 10.6
P. purbeckensis	1966	51.5 ± 11.4	3.43 ± 0.65	15.1 ± 2.2	87	1966 51.5	1966 3.43	1968 15.2
	1967	45.7 ± 10.7	3.24 ± 0.48	14.2 ± 2.8	49	1968 47.1	1967 3.24	1966 15.1
	1968	47.1 ± 8.9	3.12 ± 0.49	15.2 ± 2.5	75	1967 45.7	1968 3.12	1967 14.2
	1969	45.5 ± 8.0	3.54 ± 0.50	12.8 ± 1.9	50	1969 45.4	1969 3.54	1969 12.8
	1970	30.0 ± 9.2	2.76 ± 0.62	9.9 ± 1.9	50	1970 30.0	1970 2.76	1970 9.9
P. monticola	1966	36.7 ± 7.7	2.47 ± 0.38	14.9 ± 2.6	77	1966 36.7	1969 2.52	1966 14.9
	1967					1970 33.9	1966 2.47	1970 13.7
	1968	26.6 ± 7.7	2.29 ± 0.36	11.6 ± 2.9	97	1969 33.7	1968 2.29	1969 13.4
	1969	33.7 ± 9.8	2.52 ± 0.55	13.4 ± 3.9	23	1968 26.6	1970 2.19	1968 11.6
	1970	33.9 ± 9.4	2.19 ± 0.33	13.7 ± 2.2	43			

Table 3 (continued)

Spider species		Number of eggs	Dryweight of carapace mg	Number of eggs per mg carapace (dryweight)	Number of specimens	Number of eggs	Carapace dryweight	Number of eggs per mg carapace dryweight
P. lugubris	1966	40.2 ± 7.7	3.25 ± 0.71	12.5 ± 1.7	92	1970 40.5	1970 3.63	1966 12.5
	1967					1966 40.2	1966 3.25	1970 11.4
	1968	33.9 ± 6.1	3.11 ± 0.63	11.1 ± 1.8	90	1969 39.8	1968 3.11	1968 11.1
	1969	39.8 ± 6.7			36	1968 33.9		
	1970	40.5 ± 8.2	3.63 ± 0.64	11.4 ± 2.4	43			
P. palustris	1966	42.5 ± 8.1	2.83 ± 0.43	15.2 ± 2.1	85	1968 54.2	1968 3.03	1968 18.0
	1968	54.2 ± 6.9	3.03 ± 0.36	18.0 ± 2.4	29	1966 42.5	1966 2.83	1966 15.2

Table 4. Data on second egg sacs, compared with data on first egg sa cs from the same locality. Any two values not flanked by the same line are significantly different

Spider species		Number of eggs	Dryweight of carapace	Number of eggs per mg carapace dryweight	Number of specimens	Number of eggs in second egg sac as % of the first egg sac
P. amentata	1st egg sac	84.3 ± 14.5	5.69 ± 0.81	14.9 ± 1.9	56	64.5
	2nd egg sac	54.4 ± 13.3	5.74 ± 1.08	9.7 ± 2.5	39	
P. pullata	1st egg sac	33.4 ± 6.6	2.43 ± 0.43	13.6 ± 1.8	46	58.4
	2nd egg sac	19.5 ± 5.4	2.41 ± 0.62	8.1 ± 1.9	17	
P. nigriceps	1st egg sac	31.9 ± 5.2	2.88 ± 0.43	11.3 ± 1.6	40	52.7
	2nd egg sac	16.8 ± 4.4	2.58 ± 0.53	6.6 ± 1.6	33	
P. monticola	1st egg sac	33.9 ± 9.4	2.19 ± 0.33	13.7 ± 2.2	43	64.3
	2nd egg sac	21.8 ± 6.4	2.15 ± 0.46	9.9 ± 2.1	19	

comparable. "Good" or "bad" years for size mostly do not coincide with "good" or "bad" years for egg production.

c. *Number of eggs per mg carapace dryweight*

This value is also rather constant in all species. Striking are the extremely high values of *P. amentata* in 1966 and *P. pullata* in 1966. In both cases this high value compensates the low value in carapace dryweight, resulting in a normal number, in *P. pullata* even the highest number, of eggs. This is not the case in *P. purbeckensis* in 1970, where the effect of a low value in carapace dryweight on egg production is strengthened by a low value in number of eggs per mg carapace dryweight.

In general there is no correlation between carapace size and number of eggs per mg carapace dryweight, as can be easily seen in comparing columns 7 and 8 of table 3.

IV. SECOND EGG SACS

In a few species samples of spiders with second egg sacs could be taken. The data are compared with samples of the first egg sac from the same locality (table 4). The number of eggs in the second egg sac is about 50 to 60 % of the number in the first egg sac. The size of the spiders (except *P. nigriceps*) is the same in first and second egg sac samples. Thus it may be concluded that the production per mg carapace dryweight is much lower for the second egg sac.

V. EVALUATION OF THE RESULTS

A summary of the data on egg production of the *Pardosa* species concerned in this paper is given in Graph 4 where the ranges of mean values from all the samples are shown for the eight species of *Pardosa*.

The differences in egg production between the species are mainly caused by differences in size. Larger species produce more eggs than smaller species.

This does not seem to hold when a species produces eggs which weigh less. In this case (c.f. *P. palustris*) more eggs are produced than should be expected on account of the size.

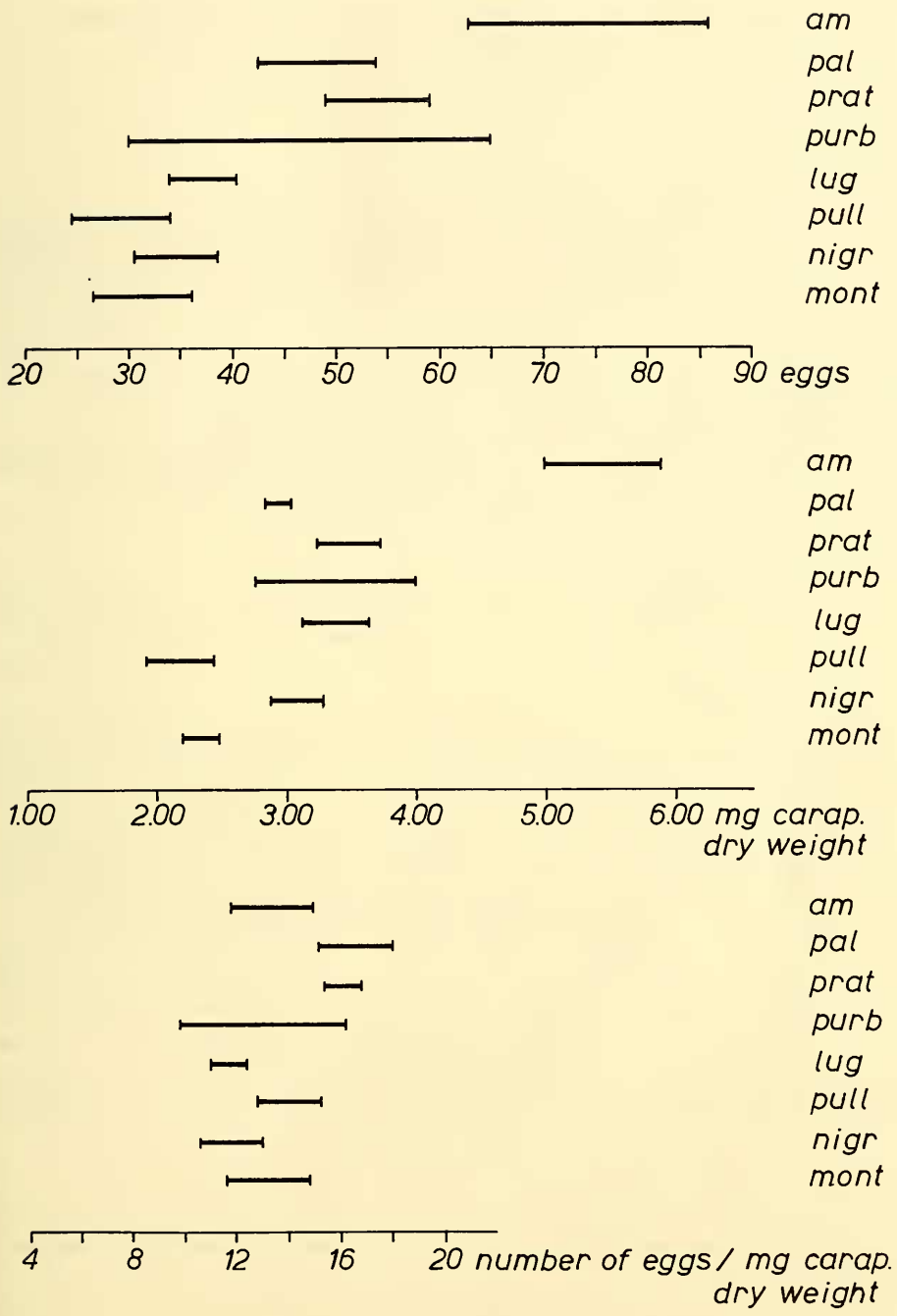
Intraspecific differences.

Differences in subsequent years in the same locality.

Any differences occurring in egg production can be caused by climate, habitat or food.

Climate. — In general the period of growing up for all species as well as their breeding periods, coincide. Therefore, the influence of good or bad weather conditions should be manifest in all species in the same way. As this is not the case, it can be concluded that no clear influence of climatic conditions can be observed.

Habitat. — In the successive years the habitats studied remained constant. This is also clear from the fact that no trend in egg production, indicating a gradual change in habitat in the course of the years, could be demonstrated. Differences in egg production, therefore, cannot be caused by differences in habitat conditions.



Graph 4. Ranges of mean values of number of eggs per egg sac, carapace dryweight and number of eggs per mg carapace dryweight, based on all samples that are discussed in this paper

Food. — Two components can be distinguished in relation to egg production:

1) Availability of the food: the total quantity of food that is available.

2) Accessibility of the food: that part of the total quantity of food that can be obtained by spiders.

Availability of the food.

One should distinguish between two periods in the life-time of a spider: the period of growing up and the egg-ripening period during the breeding season. Differences may occur in quantity of food available during the time of growing up as compared to the quantity of food available during the egg-ripening period. Large quantities of food during the time of growing up will result in large spiders. However, when during the egg-ripening period the quantity of available food is small, relatively few eggs per unit of size will be produced (e.g. *P. purbeckensis* in 1969 in table 3).

It is also possible, that small specimens produce much more per unit of size than the larger specimens, indicating that the food situation is better during the breeding season than during the time of growing up (e.g. *P. amentata* in 1966 in table 3).

Accessibility of the food.

Differences in density of the spiders can be of importance here, as higher densities of spiders will mean a smaller amount of food for every individual. Though no pertinent observations have been made on this point, there are no reasons to assume that there are considerable differences in density from year to year.

If there is enough food available the possibility remains that the animals periodically lack opportunities to catch food. Under high temperatures ($\pm$ 40° C) the spiders become inactive and this diminishes the chance of meeting prey. At the same time metabolic processes continue and, at a certain moment, the animals are due to produce an egg sac (Kessler, 1969). At low temperatures ($\pm$ 10° C) the spiders are inactive too, and although metabolic processes are retarded then, they do not stop entirely. This causes the same effect, though on a lesser scale, as in the forementioned case.

The same reasoning probably holds for the period between two moults. The length of time between two moults is, as is the case with the egg-ripening period, mainly determined by temperature. Food plays a minor role in this process (Turnbull, 1965).

In conclusion we may state, that in the same habitat in different years, differences in size of the spiders and differences in egg production per unit of size are caused by differences in food intake of the spiders. In general this does not lead to considerable differences in the mean number of eggs per egg sac.

Differences between localities in 1968.

As all three factors mentioned, viz., climate, habitat and food, might be of influence, they are evaluated here.

Climate. — There are certain differences in macroclimate between the different localities (e.g. Schiermonnikoog in the north of the Netherlands, Oostvoorne in the south). It is not clear if these differences are also reflected in differences in microclimate between the localities.

Habitat. — The clear difference in habitat in some localities, (e.g. *P. purbeckensis*

in salt marshes and in new polders; *P. amentata* in waste land and along ditches in meadows; table 2 also shows clear differences in egg production.

Food. — It is assumed that any differences in climate and difference in habitat structure in most cases only can have influence on egg production via food.

It is evident that not in all places the egg potential of the species is realized in an optimal way. This provides an opportunity to evaluate habitats as suitable or unsuitable for the development and the egg production of *Pardosa* species. However, it is not clear whether a large size and a high egg production can be considered an advantage or a disadvantage for the population of a species (e.g. *P. amentata* in a piece of waste land, table 2; the egg production and the size show low values, whereas the density of the population is rather high).

Second egg sac.

Not all species construct a second egg sac, at least not in large quantities. The meaning of the second egg sac for the survival of the species is not clear.

The lower number of eggs in second egg sacs compared with first is probably caused by a lower potential number of eggs for the second egg sac. This can be deduced from laboratory experiments (unpublished data), where the spiders consumed less food during the second egg-ripening period, as compared with the first egg-ripening period, under the same experimental conditions.

General conclusions.

There are specific differences in size. The size determines the egg potential of the spider. The size is determined by the quantity of food consumed by the spider. This is influenced by the geographical position of the habitat (differences in climate) and differences in habitat structure.

For the effectuation of the egg potential (egg production per unit of size) the same can be said. However, differences in weight of the eggs can decrease or increase the egg potential of a species as compared to other species.

In determining size and effectuation of egg potential, food is the most important factor.

VI. DISCUSSION

Dahl (1908) gives some data on number of eggs per egg sac in *Pardosa* species, with references to several authors. Wiebes (1959) describes the number of eggs in *Pardosa* species, and Den Hollander (1971) and Richter et al. (1971) do the same especially with regard to *P. pullata* and *P. prativaga* in the Netherlands. Graefe (1964) gives some information on a few *Pardosa* species from Germany and Petersen (1950), on some species from Sweden. Edgar (1971) produces data on numbers of eggs in *P. lugubris* in Scotland. The data are summarized in table 5. There is a wide variety in number of eggs produced in a species. Partly this may be caused by the fact that some authors did not study enough specimens in definite populations to gain reliable results.

Furthermore it should be noted that the data are not discussed with reference to the size of the spider which carried egg sacs. From the present study it is clear that any

Table 5. Number of eggs per egg sac, data from literature (data from the present paper are derived from the mean values found in different populations of the species)

Spider species	Number of eggs per egg sac	Author	Country
P. amentata	60—70	Dahl (Sundevall)	Sweden
	± 50	Dahl (Blackwall)	England
	75—100	Dahl (Becker)	Belgium
	60	Dahl (Henking)	Germany
	50—70	Wiebes	Netherlands
	34	Graefe	Germany
	60—85	Kessler (present paper)	Netherlands
P. pullata	25	Dahl (Blackwall)	England
	36	Dahl (de Lessert)	Switzerland
	25—30	Wiebes	Netherlands
	26—44	Den Hollander	Netherlands
	30—37	Richter	Netherlands
	27	Petersen	Sweden
	25—35	Kessler (p.p.)	Netherlands
P. prativaga	33	Graefe	Germany
	42—52	Den Hollander	Netherlands
	47—52	Richter	Netherlands
	36	Petersen	Sweden
	50—60	Kessler (p.p.)	Netherlands
P. lugubris	50	Dahl (Blackwall)	England
	40—70	Dahl (Becker)	Belgium
	25—30	Wiebes	Netherlands
	24	Graefe	Germany
	37	Edgar	Scotland
	35—40	Kessler (p.p.)	Netherlands
P. nigriceps	± 30	Wiebes	Netherlands
	30—40	Kessler (p.p.)	Netherlands
P. monticola	± 50	Dahl (Sundevall)	Sweden
	50—60	Dahl (Blackwall)	England
	30—40	Dahl (Becker)	Belgium
	± 40	Wiebes	Netherlands
	39	Graefe	Germany
	25—35	Kessler (p.p.)	Netherlands
P. palustris	± 40	Wiebes	Netherlands
	42	Petersen	Sweden
	45—55	Kessler (p.p.)	Netherlands
P. purbeckensis	30—65	Kessler (p.p.)	Netherlands

study dealing with egg production in *Pardosa* species in relation to their geographic distribution should account for the size of the spiders at the same time.

In a former paper (Kessler, 1971) I reported on the relation between food consumption and egg production of some *Pardosa* species under experimental conditions

Table 6. Comparison between experimental data on egg production (Kessler, 1971) and range of mean numbers from field samples (present paper)

Spider species	Experiments			Field samples	
	Number of eggs	Carapace dryweight	N	Number of eggs	Carapace dryweight
P. amentata	85.4	7.65	10	62.9—86.2	5.00—5.90
P. lugubris	46.8	4.59	4	33.9—40.5	3.11—3.63
P. palustris	63.0	4.38	4	42.5—54.2	2.83—3.03
P. monticola	51.0	4.64	4	26.6—36.7	2.19—2.47

in the laboratory. The spiders were kept separately in glass jars and were given an abundant food supply of *Drosophila melanogaster*.

The results of these experiments show much higher values in egg production than found in the field samples. Table 6 summarizes these differences. The most striking is the large size of the spiders in the experiments. The higher amount of eggs produced must be considered a natural consequence of this larger size. The question is why these animals were so much larger than the animals in the field samples. They have been caught in the same localities in which the field samples were collected. All experimental animals, however, were kept for some weeks in the laboratory before moulting to adults. During that time they were also given an abundant food supply. This can account for their larger size, assuming that in nature, during the period before moulting to adults (very early spring), they are not able to catch abundant food. There is evidence (Turnbull, 1962, 1965), that spiders when given small amounts of food go on growing and moulting, although the period between two moults is much longer and the spiders stay smaller. These observations indicate that, under field conditions, indeed food may be a limiting factor in egg production, directly or via the size of the spiders. In the same paper (Kessler, 1971) the reaction was described of *Pardosa* species on increasing food shortages after moulting to adult.

It was clear that all four species (viz., *P. amentata, P. lugubris, P. palustris* and *P. monticola*) adapt their egg production to the food supply. However, *P. amentata* and *P. monticola* showed a quicker reaction than *P. palustris* and *P. lugubris*. The egg-ripening period, viz., the length of the period between moulting and egg laying, proved to be mainly dependent on "climate", not on food.

The species concerned also showed the tendency to produce lighter eggs under conditions of food shortage. This phenomenon slightly compensated the lower amount of egg biomass produced.

Combining the results of Turnbull (1962, 1965), my experimental results (Kessler, 1971) and the field data from the present paper, it can be stated that:

1. The size of the adult spider is dependent on the quantity of food available during the developmental period. Conditions of climate and habitat probably influence the availability of food during this period.

2. The quantity of food available during the egg-ripening period then determines the effectivity of the potential number of eggs, that can be deposited according to size. By a decrease in weight of the individual eggs the potential number of eggs can be increased. The amount of egg production in combination with the size of the adult

spiders can give an indication of the suitability of the particular locality where the species is sampled.

Den Hollander (1971) states that, although there is a rather sizable difference in number of eggs in the first egg sac between *P. pullata* and *P. prativaga,* the difference is annihilated by the fact that the species with fewer eggs in the first egg sac (*P. pullata*) produces a second egg sac more often than *P. prativaga.* No direct data on the other species in this paper are available, but indirect data (e.g. the much greater effort to sample second egg sacs of *P. amentata* compared with *P. nigriceps*) indicate that this phenomenon may be of common interest in spiders of the genus *Pardosa.*

Before speculating on the meaning of the higher number of eggs in the first egg sac in bigger species, more data on the second egg sac of *Pardosa* species should be available.

SUMMARY

The egg production of eight *Pardosa* species (Araneae, Lycosidae) in the Netherlands is described on the basis of field samples. The eggs are deposited in an egg sac, which is carried around by the female spider on the spinnerets.

The first egg sac seems to be the most important one for reproduction, although some species sometimes produce a second egg sac, containing much less eggs than the first. The mean number of eggs in the first egg sac ranges from ± 86 in *Pardosa amentata* to ± 25 in *Pardosa monticola.* The number of eggs produced is dependent on the size of the spiders.

Intraspecific differences occur as to the number of eggs and size of the spiders between populations from different localities in the same year. In the same locality no obvious differences in egg production could be found in subsequent years in different species.

It is concluded that differences in size and differences in egg production between populations are mainly caused by differences in food intake of the spiders.

ACKNOWLEDGEMENTS

I should like to thank Prof. Dr. L. Vlijm for his valuable criticism and help during the investigations and with preparing the manuscript. I am deeply indebted to Mrs. M. N. Giardina-Wind and Mr. S. C. Verhoef for their help in collecting numerous data on egg sacs and spiders. I am indebted to Mr. G. W. H. van den Berg for drawing the figures and to many other people for their assistance in collecting spiders.

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